Morphological and histological study of the hyperostoses of *Lepidopus albyi* (Sauvage, 1870), a fossil Trichiuridae from the Tortonian (Upper Miocene) of Piedmont (Italy)

by

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ABSTRACT. - Two fossil specimens of the cutlassfish *Lepidopus albyi,* from the Tortonian (Upper Miocene) of Piedmont (Italy) showed hyperostotic pterygiophores. The comparative morpho-histological study of this material with the fossil *L. proargenteus* and the living *Trichiurus lepturus* showed that the swollen bones are constituted of spongy bone in the three species. This hyperostosis results from a double process: an increase of the periosteal osteogenesis combined to an important resorption that creates numerous vascular cavities. The factors that control this hyperostotic phenomenon in scabbardfishes were probably the same in the Tortonian time as today. However, they remain hypothetical, even if an epigenetic hydro-mechanical constraints or genetic factors seem the more likely. In contrast, a physiological response to survival in an extreme biocenosis with salt excess should be rejected. Whatever the causal factors involved, the hyperostotic phenomenon is an old one in this teleost family, that is at least 8.8 My old.

RÉSUMÉ. - Étude morphologique et histologique des hyperostoses de *Lepidopus albyi* (Sauvage), un Trichiuridae fossile du Tortonien (Miocène supérieur) du Piémont (Italie).

Deux spécimens de l'espèce de sabre fossile, *Lepidopus albyi*, du Tortonien (Miocène supérieur) du Piémont (Italie) présentaient des ptérygiophores hyperostosés. Une étude morpho-histologique comparée de ce matériel fossile avec un autre fossile *L. proargenteus* et l'espèce actuelle *Trichiurus lepturus*, a montré que les éléments hyperostosés sont essentiellement constitués d'une spongiosa osseuse. L'hyperostose résulte d'une intensification des processus d'ostéogenèse du tissu périostique, suivie d'une importante érosion donnant ainsi naissance à un tissu osseux spongieux. Les facteurs qui seraient responsables de ce phénomène d'hyperostose, caractéristique chez les Trichiuridae, restent hypothétiques, même si un facteur épigénétique tel qu'une contrainte hydromécanique ou des facteurs génétiques sont les plus probables. Dans le cas présent, l'hypothèse d'un processus physiologique hyperostosant comme réponse adaptative à des conditions écologiques extrêmes (excès de sels dans le milieu) doit être rejetée. Nos observations confirment l'ancienneté du processus d'hyperostose dans cette famille de Téléostéens, au moins 8,8 Ma.

Key-words. - Trichiuridae - *Lepidopus* - *Trichiurus* - Italy - Tortonian - Fossils - Hyperostosis - Ossification - Paleohistology.

The Tortonian outcropping near Alba (Piedmont, Italy), in the flood plain of the Tanaro River (Fig. 1), consists of an alternance of massive marls and of thinly laminated intercalations that have yielded skeletons of fossil fishes (Gaudant, 2009). A new fossiliferous outcrop situated in the territory of the municipality of Roddi (Ro 1) was investigated by one of us (E.B.) who collected there a small fish fauna including *Alosa elongata* Agassiz, 1844, *Myctophum dorsale* (Sauvage, 1870), *Lepidopus albyi* (Sauvage, 1870), *Belone* sp., *Scorpaena* sp., etc. With the exception of *Scorpaena* sp., all the identified species were already known in the Tortonian of the surroundings of Alba. However, the two specimens of *Lepidopus albyi* (Sauvage, 1870), which were discovered at this spot differ from the other specimens of the same species previously collected near Alba (Gaudant *et al*., 2007), as the pterygiophores of their dorsal fin exhibit remarkable signs of hyperostosis, whereas the three specimens previously found in the territory of Alba are not affected at all.

From a morphological point of view, hyperostosis is an important thickening of some specific bones that take a swollen aspect (Köstler, 1882; Chabanaud, 1926; Bertullo and Traibel, 1955; Olsen, 1969, 1971; Desse *et al*., 1981; Meunier and Desse, 1986; Gauldie and Czochanska, 1990; Smith-Vaniz *et al*., 1995; Meunier *et al*., 1999). This thickening results from a significant increase of the periosteal ossification of the bones that is generally accompanied, in fishes, with an active resorption of the bony tissues giving rise to spongy bone that constitutes the very main part of the

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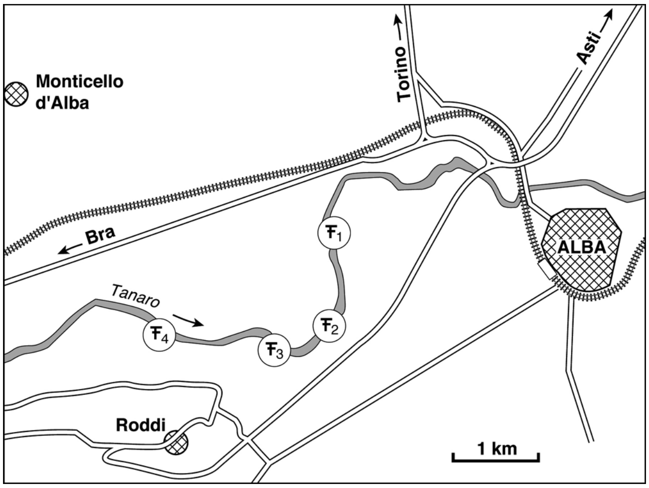

Figure 1. - Map of the surroundings of Alba (Piedmont, Italy), showing the different Tortonian outcrops of the Tanaro River bed having yielded fish skeletons. The locality Ro 1 is noted F4.

swollen bone (Desse *et al*., 1981; Meunier and Desse, 1994; Meunier *et al*., 1999; Béarez *et al.,* 2005). However, in some small species the resorbing process is lacking or limited, and hyperostotic bones are only made of compact bony tissue either vascularized as in *Sardina? crassa* (Sauvage, 1873) and *Gobius ignotus* Arambourg, 1927 (Gaudant and Meunier, 1996) or not vascularized as in *Aphanius crassicaudus* (Agassiz, 1839) (Meunier and Gaudant, 1987).

Fossil hyperostotic bones are known in several taxa: the cyprinodontid *Aphanius crassicaudus* from the Mediterranean Miocene (Meunier and Gaudant, 1987), the clupeid *Sardina? crassa* and the gobioid *Gobius ignotus* from the Upper Miocene of Algeria (Gaudant and Meunier, 1996), the Cyprinid *Hsianwenia wui* Chang *et al*., 2008 in the northern Tibetan Plateau (Chang *et al*., 2008) and an undetermined cichlid (Schlüter *et al*., 1992). The swollen bones show a compact bony tissue in *Aphanius crassicaudus* (Meunier and Gaudant, 1987) and in the cichlid (Schlüter and Kohring, 2002), two acellular bony fishes, and in the cellular bone fish *Sardina? crassa* (Gaudant and Meunier, 1996), and not spongy bone contrary to the data concerning hyperostotic bones of fossil (Fierstine, 1968; Hewitt, 1983) or extant (Meunier and Desse, 1994; Meunier *et al*., 1999; Béarez *et al*., 2005) various perciformes. As in *L. albyi*, hyperostotic bones are restricted to pterygiophores only, we can postulate that hyperostosis is there constituted of spongy bone. So it was interesting to study the histological organization of hyperostotic pterygiophores of the fossil species *Lepidopus albyi*, an acellular bony fish, in order to verify the histological characteristics of this new hyperostotic fossil material.

The morphological and histological study of the hyperostotic bones of the fossil *Lepidopus albyi* (Teleostei, Perciformes, Trichiuridae) confirms the spongy nature of the bones. We have compared them to the hyperostoses that affect regularly the extant *Trichiurus lepturus* Linnaeus, 1758. As other members of the trichiurid family, this species presents frequently hyperostotic pterygiophores (Gervais, 1875; Korschelt, 1940; Bhatt and Murti, 1960; Olsen, 1971; Grabda, 1982).

MATERIAL AND METHODS

Material

Fossil material. - *Lepidopus albyi* from the Tortonian of Roddi, Piedmont (at least 8.8 My; Gaudant, 2009): two incomplete specimens kept at Alba in the paleontological collections of the Civico Museo "F. Eusebio": G. 1594/1 and G. 1594/2 (Figs 2, 3).

Comparative fossil material. - One specimen of *Lepidopus proargenteus* Arambourg from the Messinian of Oran - Raz el Aïn: cf. Arambourg (1927, pl. 30, fig. 1); fragment of *Lepidopus* skeleton (MNHNP, LRC 128) found in the middle part of the Messinian diatomitic sequence exposed in the Serrata of Lorca (Lorca basin, Murcia Province, Spain) (Fig. 4A); fragment of body assigned to the genus *Lepidopus*, found in the Messinian Chicamo cycles of Abanilla, Fortuna Basin, Spain (Gaudant, unpubl.) (Fig. 4B).

Extant material. - Isolated bones of *Trichiurus lepturus*: one specimen, that is about 100 cm long. Five hyperostotic pterygiophores were sampled, boiled in water to remove flesh; and were then dried up (Fig. 5).

Methods

One pterygiophore of *Lepidopus albyi* was embedded in stratyl polymer (Chronolita 2195). Transverse and longitudinal sections were cut with a sawing machine and ground down.

The pterygiophores of *Trichiurus lepturus* were dehydrated through a series of graded alcohols, followed by acetone, then cleared in styrene and embedded in stratyl polymer. Transverse and longitudinal sections were obtained as for *Lepidopus* material (Fig. 5).

The sections were observed under the microscope in transmitted natural and polarized lights.

RESULTS

Morphological data

The fossil specimen of *Lepidopus albyi* registered under the reference G. 1594/1 (Fig. 2) is the more complete and the best preserved one; it shows the posterior part of the head and a part of the body having a maximum depth of about 40 mm. The subtriangular operculum is sensibly wider than high. About ten fin rays of the pectoral fin are preserved. There are 40 vertebrae preserved, as well as about 40 dorsal

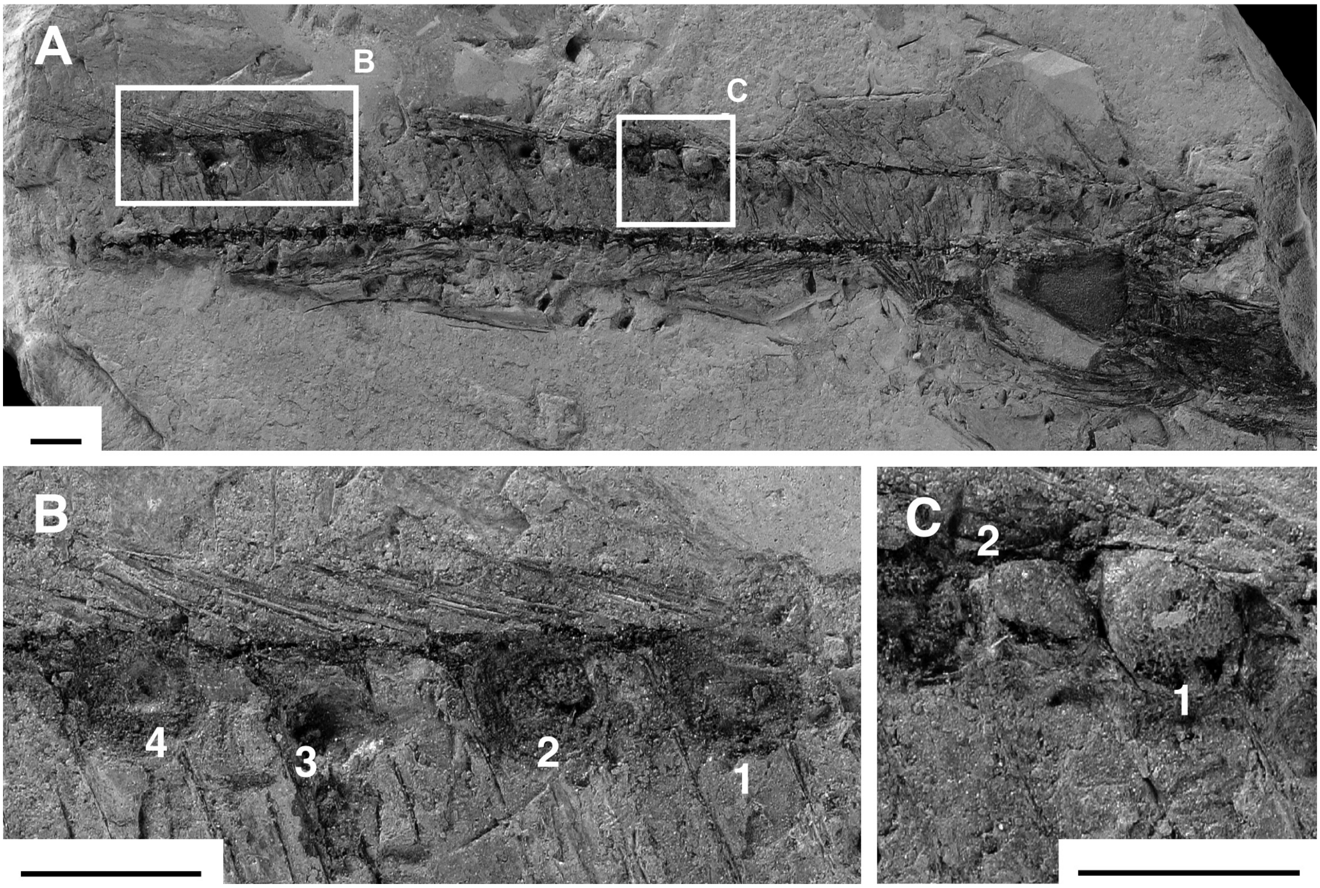

Figure 2. - *Lepidopus albyi*. **A**: General view of specimen G. 1594/1; **B**: Enlargement of figure A, showing four (1-4) hyperostotic pterygiophores; **C**: Enlargement of figure A, showing two (1-2) hyperostotic pterygiophores. Scale bars = 1 cm.

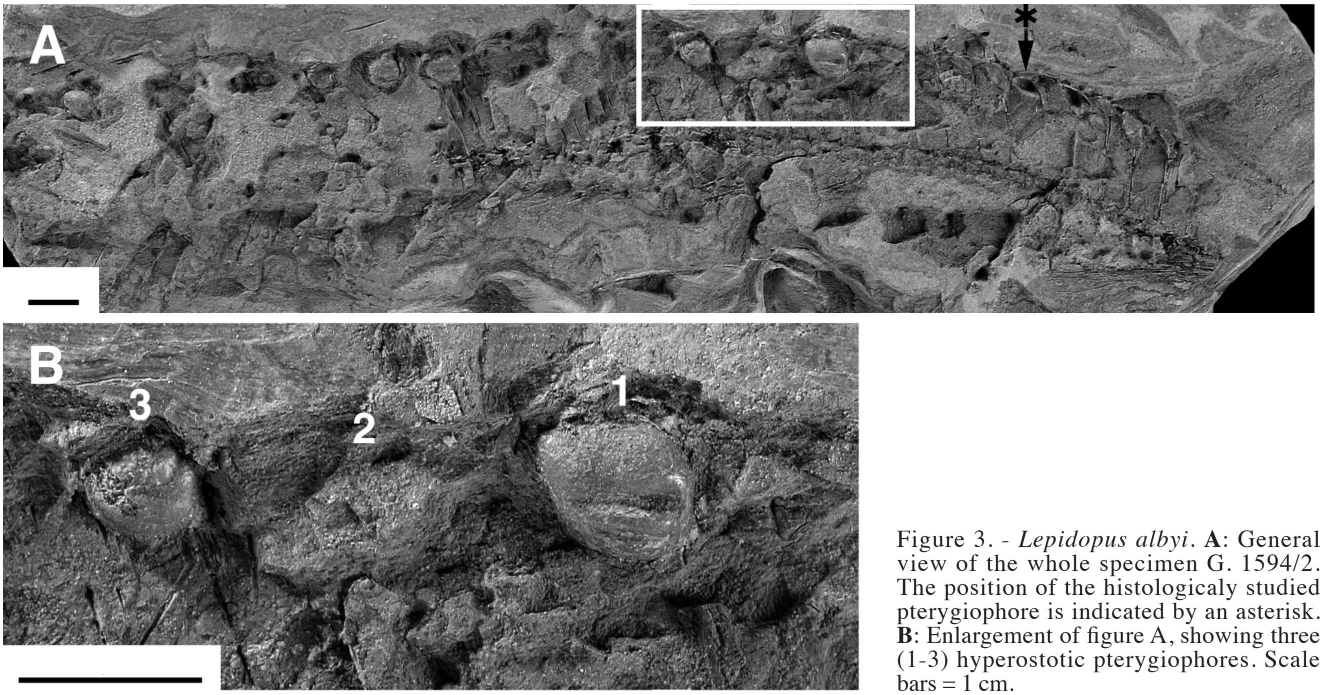

Figure 3. - *Lepidopus albyi*. **A**: General view of the whole specimen G. 1594/2. The position of the histologicaly studied pterygiophore is indicated by an asterisk. **B**: Enlargement of figure A, showing three (1-3) hyperostotic pterygiophores. Scale bars = 1 cm.

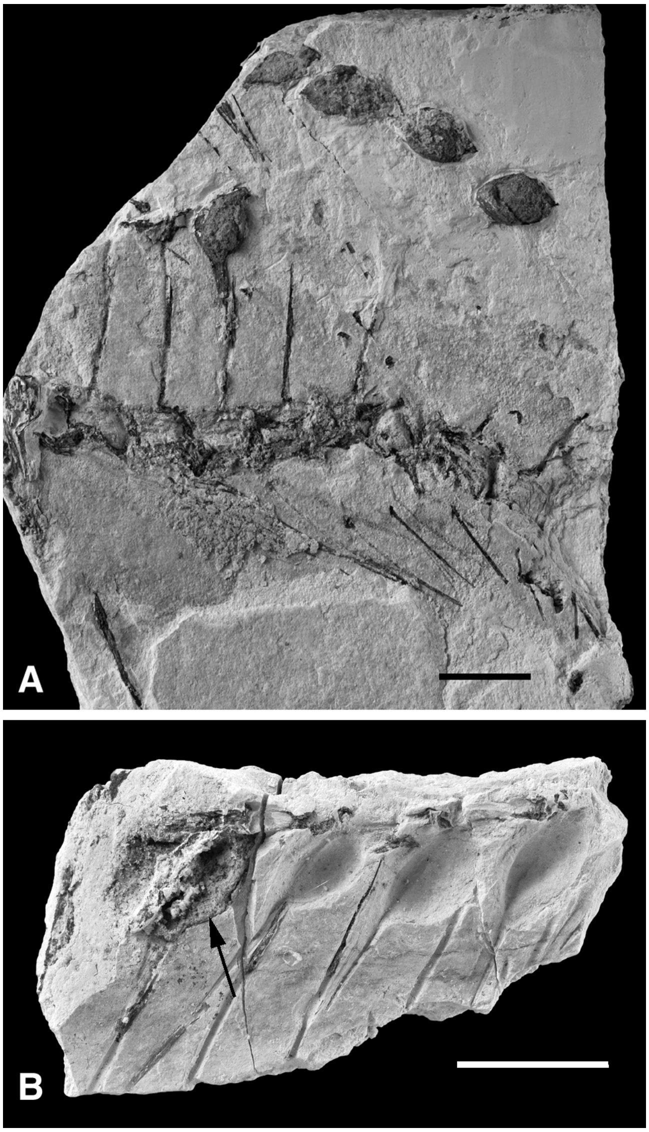

Figure 4. - *Lepidopus* sp. **A**: Body fragment (specimen MNHNP, LRC 128) showing a series of hyperostotic pterygiophores of the dorsal fin. Preevaporitic Messinian of the Lorca Serrata (Murcia Province, Spain); **B**: Part of the dorsal fin showing an hyperostotic pterygiophore (arrow) and three impressions (asterisks). Preevaporitic Messinian ("Chicamo cycles") of the Fortuna Basin (Murcia Province, Spain). Scale bars = 1 cm.

fin rays, the first one being situated above the antero-dorsal angle of the operculum. The rays of the dorsal fin are supported by typical pterygiophores, the two parts of which make together a 120° angle. Above the operculum, four of them are remarkably inflated, as well as two other ones situated above the abdominal cavity (Fig. 2B). Backwards, one can also see the sagittal section of several hyperostotic pterygiophores (Fig. 2C).

The other fossil specimen of this species, G. 1594/2 (Fig. 3), is a fragment of body beginning just behind the head, as shown by the presence of several pectoral fin rays. The preserved section of the vertebral column includes about 40 vertebrae. Although the dorsal fin is not preserved, a series of strongly hyperostotic pterygiophores is present. The pterygiophore that is histologically studied was the anteriormost one (cf. asterisk on figure 3A).

One fossil specimen of *Lepidopus proargenteus*, from the Messinian of Oran-Raz el Aïn (see Arambourg, 1927, pl. 30, fig. 1) exhibits some hyperostotic pterygiophores in the dorsal fin. A re-examination of this specimen (MNHNP, ORA 168) has shown that there are 5 hyperostotic pterygiophores in the forepart of the dorsal fin. They are followed by about 7 or 8 normal ones, whereas two or three hyperostotic pterygiophores are again present behind the latter, and another one is situated more posterior, after two or three normal pterygiophores. All of them are visible by their sagittal section.

The fragment of *Lepidopus* skeleton (MNHNP, LRC 128), from the Messinian diatomitic sequence exposed in the Serrata of Lorca (Lorca basin, Murcia Province, Spain), shows a dorsal fin exhibiting hyperostotic pterygiophores. One of them is preserved at its original place, near the distal extremity of a neurapophysis, whereas four other displaced nodules are preserved at a short distance above the skeleton fragment (Fig. 4A).

Finally, a fragment of a poorly preserved *Lepidopus* was recently collected in the Messinian of the Chicamo cycles (Fortuna basin, Murcia Province, Spain). This small fragment shows four typically hyperostotic pterygiophores (Fig. 4B) belonging to the forepart of the dorsal fin, three of them being preserved as negative casts in the sediment. It should be noted that, according to a preliminary examination, the fish fauna from the Chicamo cycles, looks rather similar to that of the Lorca basin (Gaudant, 1995).

Hyperostotic bones of *Trichiurus lepturus* have an olive shape and they show two sharp extensions (Fig. 5). The one at their inner part is the proximal extremity of the pterygiophore; the other one at their apex is the distal part of the pterygiophore (Fig. 5). The hyperostotic bones are obliquely inserted in the sagittal septum.

Histological data

The histological organization of the hyperostotic bones is the same in the fossil (Figs 6A-D) and extant (Figs 7A-C) material. They are essentially constituted of spongy bone surrounded by a thin cortical bony sheath (Fig. 7A). We can see in the centre of the pterygiophore a more or less axial trabecula of primary compact bone (Figs 6A, B, 7B, C) that corresponds to the initium of the pterygiophore (Grabda, 1982; fig. 7). The spongy bone spreads around this axial bone.

The bony tissues of the whole bone are all deprived of bone cell lacunae; they are of acellular type. The cavities of the spongy bone are relatively large and they are limited by thin bony trabeculae (Figs 6A, B, 7B, C); some of these

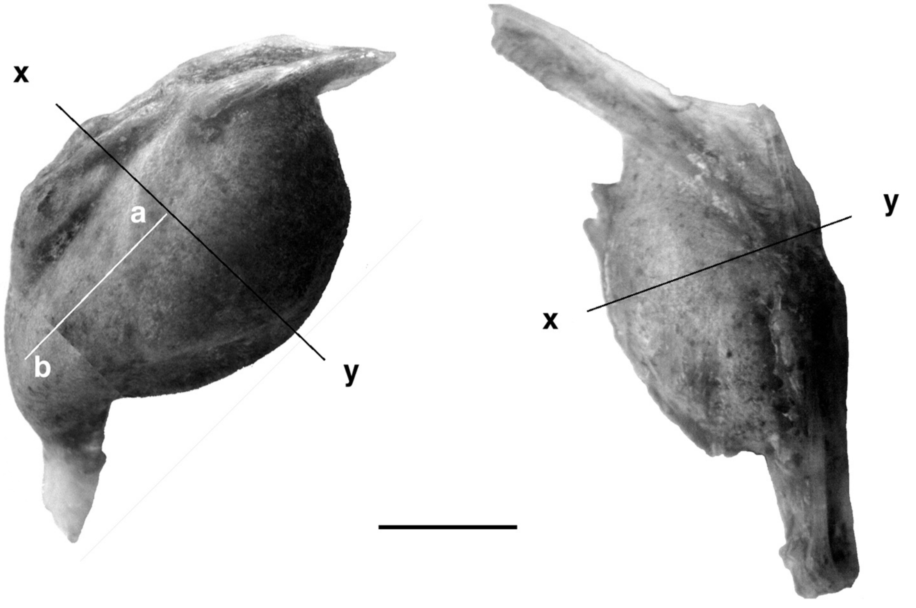

Figure 5. - *Trichiurus lepturus*. Two hyperostotic pterygiophores. The lines **xy** and **ab** correspond to the transverse and longitudinal sections in Fig. 7, respectively. Scale bar = 2 mm.

walls have an irregular surface with Howship's lacunae indicating resorption processes (Fig. 6C). Here and there, secondary bone can be observed owing to its fibrillary matrix that is clashing on the primary bone matrix and the presence of cementing lines (Fig. 6D).

The initium of the pterygiophore had supported the osteogenic process that gave rise to its swelling. As osteogenesis progresses, an erosive osteoclastic activity has progressively replaced the primary bone by secondary spongy bone. So the compactness of the hyperostotic bone is less important than if it was constituted of compact primary bone.

DISCUSSION

Hyperostotic bones are relatively scarce in the fossil record. Yet some various cases have been described in the following taxa: Clupeidae (Gaudant and Meunier, 1996), Cyprinidae (Chang *et al*., 2008), Cyprinodontidae (Meunier and Gaudant, 1987), Carangidae (Fierstine, 1968), Cichlidae (Schlüter *et al*., 1992), Tetraodontidae (Tyler *et al*., 1992). On the contrary, numerous descriptions of hyperostosis are known in extant teleosts (Gervais, 1875; Starks, 1911; Bertullo and Traibel, 1955; Chabanaud, 1926; Olsen, 1969, 1971; Desse *et al*., 1981; Grabda, 1982; Meunier and Desse, 1986; Meunier *et al*., 1999, etc.). Some taxa are particularly affected, either at the family level such as Carangidae, Sciaenidae and Sparidae (Gauldie and Czochanska, 1990; Smith-Vaniz *et al*., 1995), or at the species level (Smith-Vaniz *et al*., 1995). Hyperostosis has been used by taxonomists as a taxonomical tool (Johnson, 1973; Weiler, 1973; Gauldie and Czochanska, 1990; Smith-Vaniz *et al*., 1995; Smith-Vaniz and Carpenter, 2007; etc.) and by archeoichtyologists (Olsen, 1969; Driesch, 1994; Béarez, 1997) as accurate diagnostic criterion. In extant teleosts, large number of bones can be affected by hyperostosis, but in a given species only a few ones, and generally the same, are hyperostotic.

The hyperostotic process was first considered as affecting only marine fish species possessing acellular bone (Desse *et al*., 1981; Meunier and Desse, 1986), but some cases of hyperostosis affecting species with cellular bone were more recently described in fossil [Clupeidae (Gaudant and Meunier, 1996), Cyprinidae (Chang *et al*., 2008)], and in extant taxa [Thunninae (Béarez *et al*., 2005), and Ariidae: for example the marine Pacific catfishes *Bagre pinnimaculatus* (Guzmán and Polaco, 2002) and *B. panamaensis* (Meunier and Béarez, unpubl. results)].

What are the causality and the biological significance of the hyperostotic phenomenon in these various species? There is no clear explanation for any hyperostotic case recorded so far, but some hypotheses were proposed: help in fin erection, or in neutral buoyancy, ageing action on bone, reaction to high temperatures, metabolic abnormality, ionic poisoning, fungic infestation, tumorous phenomenon, genetic factors, etc. (see review in Meunier and Desse, 1986). At first, we must point to two structural features of hyperostosis in teleost fossil. The one concerns small species such as *Aphanius crassicaudus*, *Gobius ignotus*, and *Sardina? crassa*, in which the process concerns the greatest part of the skeleton, where hyperostotic bones are constituted of compact bone (Meunier and Gaudant, 1987; Gaudant and Meunier, 1996). These species lived in waters oversaturated with calcium combined with other ions. For these species, we can suggest that hyperostosis could be a detoxication process favouring fixation of the ionic excess in the skeleton as it is hypothesized for the fossil cichlids from the phosphorites of the Lake

Manyara area that contain excess of fluor. "The development of these structures is probably correlated with the high content of fluorine in this exceptional environment and denotes a physiological survival strategy in this ancient biocenosis" (Schlüter and Kohring, 2002). Unfortunately, we do not know any study that mentions an hyperostosis generalised to the whole skeleton in teleosts currently living in hyperosmotic waters. To our knowledge, the only work supporting the hypothesis of a hyperionic factor is the observation by Greenwood (1992) on the cichlid *Tilapia guinasana* Trewavas, 1936. This tilapiine lives in the thermal soda-lakes of East Africa and shows a typical "hyperosteosis" (sic) feature that concerns mainly the cranial skeleton with inflated frontals, epiotics and the basal side of the ventral pharyngeal jaw. According to Greenwood, "the general appearance of these skull regions (dorsicranium) in *T. guinasana* is thus one of moderate inflation and roundness, especially when compared with the skull roof in *T. sparrmanii* Smith, 1840 of a similar size", a close-related species (Trewavas, 1936). This inflation of frontals and epiotics results from a hyperdevelopment of spongy bone (Greenwood, 1992). For this author "one possible explanation for the occurrence of hyperosteosis in *T. guinasana* is that of environmental induction. Lake Guinas water has a very high calcium carbonate content (calcium hardness, as $CaCO_3$, 185 ppm), an environmental factor to which the fishes might have responded, physiologically, by increasing the volume and calcification of certain bones." Moreover, Greenwood raised four specimens of *T. guinasana* (part of an F1 generation derived from wild-caugth parents) in tap water ($CaCO_3$, 45 ppm). "In all four fishes the overall morphology of the dorsocranium is nearer that of similar sized wild-caught *T. sparrmanii* than of *T. guinasana,* thinner and less spongy. This indicates the possibility that "such environmental factors as water chemistry may influence the structure of certain skull roofing bones"(sic).

The second alternative concerns species living in a normal (?) marine environment and whose hyperostosis confers to the bone a spongy structure. Moreover, even if the hyperostotic phenomenon can affect various bones of the skeleton in a given species, it is never as extended as it is in the precedent group. So we consider that the causal factors in the different fossil material cannot be the same and that the hyperostosis in *L. albyi* probably have the same various ori-

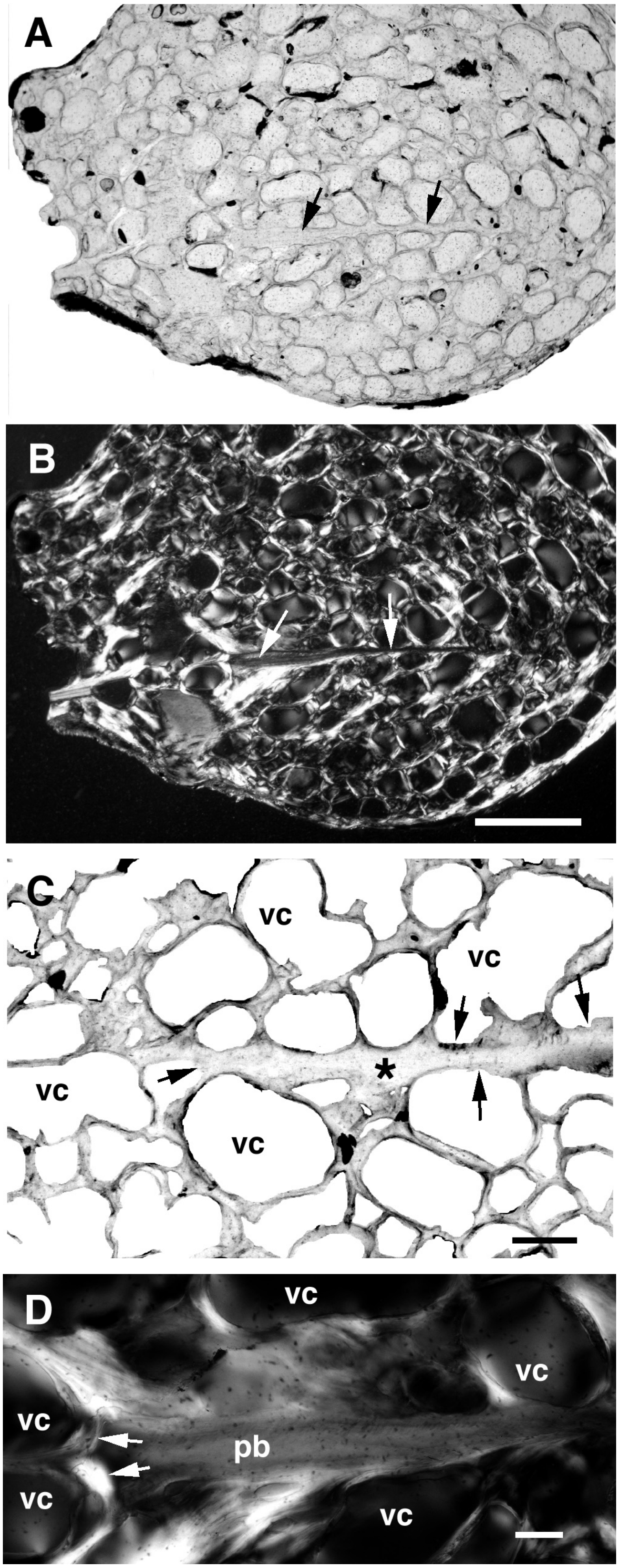

Figure 6. - *Lepidopus albyi*. Longitudinal sections of an hyperostotic pterygiophore. **A**: Transmitted natural light; **B**: Transmitted polarized light. The arrows point to the axial skeleton of the pterygiophore. Hyperostotic spongy bone can be seen on each side of the axial skeleton. Scale bar = 200 μm; **C**: Transmitted natural light. Detail showing the vascular cavities (**vc**) and thin bony trabeculae. The arrows point to eroded regions on the axial part (asterisk) of the pterygiophore. Scale bar = 150 μm); **D**: Transmitted polarized light. Secondary bone is clearly observable (arrows) at the left part of the axial primary bone as shown by the clear lines of resorption. Scale bar = 50 μm.

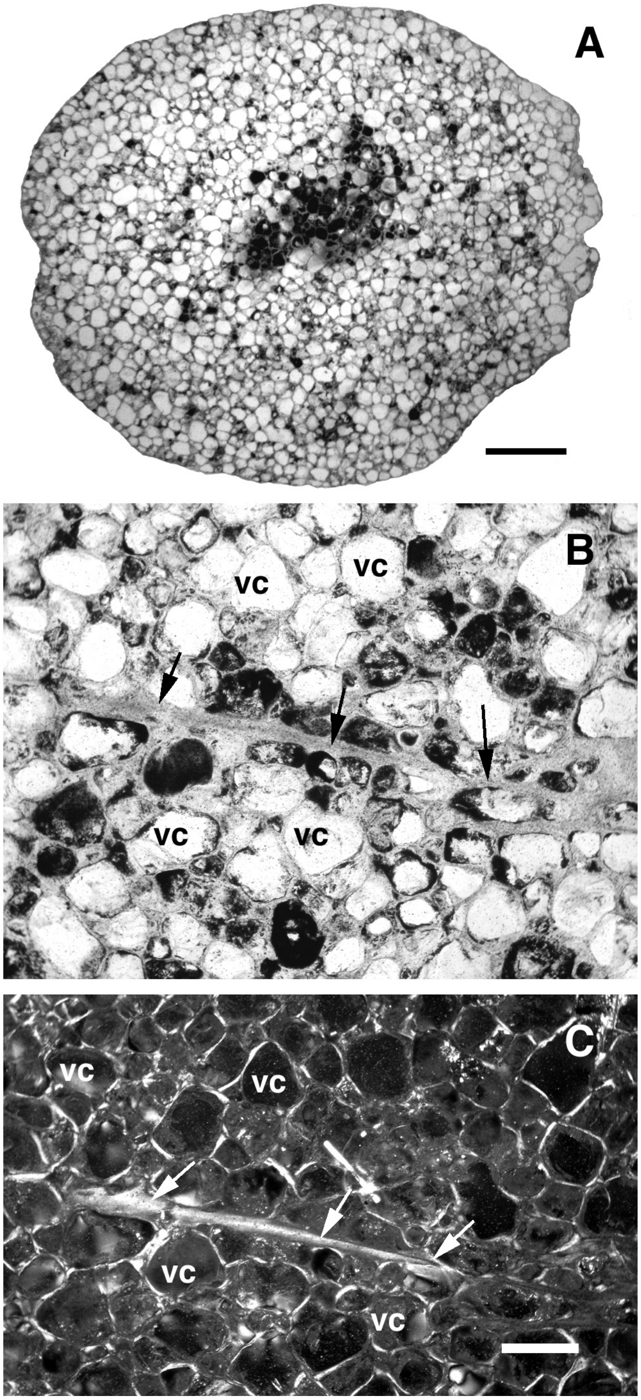

Figure 7. - *Trichiurus lepturus*. **A**: Transverse section of the hyperostotic pterygiophore (transmitted natural light). The pterygiophore is constituted of a regular spongy bone without a surrounding cortical layer. Scale bar = 1 mm; **B**: Longitudinal section (transmitted natural light); **C**: Same section as in B (transmitted polarized light). The arrows point to the axial skeleton of the pterygiophore. The organisation of the hyperostotic bone is the same as in the fossil material (see Fig. 6) (**vc** = vascular cavities). Scale bars = 100 μm.

gins as the hyperostosis of extant species. The hyperostosis of *Lepidopus albyi* belongs to the second type.

Except for Bhatt and Murti (1960) and Selvaraj *et al.* (1973), the authors agree that hyperostoses are not pathological formations (Olsen, 1971; Desse *et al.*, 1981; Gauldie and Czochanska, 1990). It also appears that fishes with such swollen bones show a normal behaviour (Johnson, 1973). For example, hyperostotic processes seem inescapable in the jack mackerel, *Trachurus trachurus* (Carangidae), since a high number of individuals show swollen bones at the end of their life (Desse *et al.*, 1981). As these fishes do not show abnormal behaviour, we can consider that the phenomenon is not pathologic, at least in this species and, possibly, in the whole carangid family since a lot of carangids have hyperostotic bones (Smith-Vaniz *et al.*, 1995; Smith-Vaniz and Carpenter, 2007). We think that it is the same in the triglid *Prionotus stephanophrys* (Meunier *et al.*, 1999) as in the scombrid *Euthynnus alleteratus* (Béarez *et al.*, 2005) in which the whole adult specimens have always the same hyperostotic bones.

The bones affected by hyperostosis increase in size (possibly in number for some species) along the growth of the fish (Desse *et al.*, 1981; Meunier and Gaudant, 1987; Gauldie and Czochanska, 1990), but the correlation between these factors seems low (Gauldie and Czochanska, 1990); to our knowledge there are not quantitative studies to validate this hypothesis. The more intensive analytical studies were made on the skipjacks *Trachurus trachurus* and *T. mediterraneus* (Desse *et al.*, 1981; Laroche *et al.*, 1982) and the sparid *Chrysophrys auratus* (Gauldie and Czochanska, 1990). These studies failed to show any significant differences between normal and hyperostotic bones. For example, there was no difference in fatty acid composition between the hyperostotic and normal vertebrae in *Chrysophrys auratus* (Gauldie and Czochanska, 1990) whereas Breder (1952) suspected that fat in bones might play an important function. In the same way, there are no significant variations of several blood parameters linked to bone histo-physiology (calcemy, phosphatemy and calcitonin content) either, nor of the physical characteristics of the bony mineral between hyperostotic bones and normal bones in *Trachurus trachurus* (Desse *et al.*, 1981; Laroche *et al.*, 1982).

We can also have a look to the fungic hypothesis of Grabda (1982), especially because it was suggested for another trichiurid: *Lepidopus caudatus* (Euphrasen, 1788). We are not convinced by the data of the author. Effectively, if a fungic infestation had induced a swelling reaction of pterygiophore bones, the mycelium would have developed microscopic channels into bony tissues. But Grabda (1982) has noticed mycelium-like formations in the medullar cavities only. Moreover, a fungic infestation would attack other bones of the fish and then these bones should also develop hyperostosis. This is neither the case for *Lepidopus caudatus* material studied by Grabda (1982) nor our extant and fossil material in which only some pterygiophores have developed hyperostosis. On our fossil and extant hyperostotic material, the internal content of the bone cavities is not preserved; but anyway, bone does not show mycelium tubules. If a fungic origin of hyperostotic phenomenon can be hypothesized here and there, we think this cannot be retained in the present case.

In the case of the hypothesis of a hydrodynamic function, an unresolved question is the fact that the hyperostotic phenomenon affects fishes that show strikingly different morphologies: for example the carangids *Caranx*, (that is high and flat) and *Trachurus* (a fusiform fish), the triglid *Prionotus* (a benthic fish), the muraenesocid *Cynoponticus* (an anguilliform fish), and the trichiurids (long ribbon-like flat fishes) are mophologically very different from one another, and it can be assumed that their swimming processes are also quite distinct (Lindsey, 1978; Webb, 1978; Meunier and Ramzu, 2006).

For the species where the hyperostotic process seems to be an "usual" condition, as in numerous carangids or as in *Prionotus stephanophrys*, a hydromechanical function linked to ageing is favoured (Desse *et al*., 1981). But to test this morpho-functional hypothesis we need quantitative studies of the evolution of the shape of fishes in correlation with data for swimming ability and concerning the development of the hyperostotic bones during their life. There might be close correlations between genetic factors (mainly highly derived teleostean species with acellular bone are affected), physiological factors (mechanical and physiological constraints on the bone) and external factors (physico-chemical parameters of sea water).

The present study has shown that a hyperostotic phenomenon with an increase of primary osteogenesis associated with an important inner resorption conferring to the bone a typical spongy structure is an old phenomenon, at least 8.8 My old.

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REFERENCES

ARAMBOURG C., 1927. - Les poissons fossiles d'Oran. *Mater. Carte Géol. Alger.*, 1re sér. Paléontol., 6: 1-298.

BÉAREZ P., 1997. - Las piezas esqueléticas diagnósticas en arqueoictiología del litoral ecuatoriano. *Bull. Inst. Fr. Etudes Andines*, 26(1): 11-20.

BÉAREZ P., MEUNIER F.J. & KACEM A., 2005. - Description morphologique et histologique de l'hyperostose vertébrale chez la thonine noire, *Euthynnus lineatus* (Teleostei, Perciformes, Scombridae). *Cah. Biol. Mar.*, 46: 21-28.

BERTULLO V.H. & TRAIBEL R.M., 1955. - Neoplasma de los peces de las costas uruguayas. I. Osteoma de la costilla pleural de la corvina (*Micropogon opercularis*). *Anal. Fac. Vet. Uruguay*, 6: 55-59.

BHATT Y.M. & MURTI N.N., 1960. - Hyperostosis in *Trichiurus haumela* (Forskal). *J. Univ. Bombay*, 28: 84-89.

BREDER C.H., 1952. - The problem of directives to cellular proliferation as illustrated by ontogenetic processes in certain fishes. *Growth*, 16: 189-198.

CHABANAUD P., 1926. - Fréquence, symétrie et constance spécifiques d'hyperostoses externes chez divers poissons de la famille des Sciaenidés. *C. R. Acad. Sci.*, Paris, 182: 1647-1649.

CHANG M., WANG X., LIU H., MIAO D., ZHAO Q., WU G., LIU J., LI Q., SUN Z. & WANG N., 2008. - Extraordinarily thick-boned fish linked to the aridification of the Qaidam Basin (northern Tibetan Plateau). *Phil. Nat. Acad. Sci.*, 105(36): 13246-13251.

DESSE G., MEUNIER F.J., PERON M. & LAROCHE J., 1981. - Hyperostose vertébrale chez l'animal. *Rhumatologie*, 33: 105-119.

DRIESCH A. von den, 1994. - Hyperostoses in fish. *In*: Fish exploitation in the Past, Proc. 7th Meeting ICAZ Fish Remains Working Group (Van Neer W., ed.). *Ann. Mus. R. Afr. Cent., Sci. Zool.*, 274: 47-53.

FIERSTINE H.L., 1968. - Swollen dorsal fin elements in living and fossil *Caranx* (Teleostei: Carangidae). *Contrib. Sci. Los Angeles,* 137: 1-10.

GAUDANT J., 1995. - Nouvelles recherches sur l'ichthyofaune messinienne des environs de Lorca (Murcia, Espagne). *Rev. Esp. Paleont.*, 10: 175-189.

GAUDANT J., 2009. - I pesci del Miocene superiore albese e la crisi ecologica del Mediterraneo. *Alba Pompeia*, n.s., 28(2007): 83-96.

GAUDANT J. & MEUNIER F.J., 1996. - Observation d'un cas de pachyostose chez un Clupeidae fossile du Miocène terminal de l'ouest Algérien, *Sardina* ? *crassa* (Sauvage, 1873). *Cybium*, 20: 169-183.

GAUDANT J., CAVALLO O., COURME-RAULT M.-D., FORNACIARI E., LAURIAT- RAGE A., LAPPARENT F. DE & MERLE D., 2007. - Paléontologie des marnes tortoniennes affleurant dans le lit du Tanaro, près d'Alba (Piémont, Italie). *Riv. Piemont. Stor. Nat.*, 28: 3-51.

GAULDIE R.W. & CZOCHANSKA Z., 1990. - Hyperostotic bones from the New Zealand snapper *Chrysophys auratus* (Sparidae). *Fish. Bull.*, 88: 201-206.

GERVAIS P.M., 1875. - De l'hyperostose chez l'homme et les animaux. *J. Zool.*, 4: 445-462.

GRABDA E., 1982. - Fungi-related outgrowths on pterygophores of single fins of *Lepidopus caudatus* (Euphrasen, 1788) (Pisces: Trichiuridae). *Acta Ichthyol. Piscat.*, 12(1): 87-105.

GREENWOOD P.H., 1992. - A redescription of the uniquely polychromatic African cichlid fish *Tilapia guinasana* Trewavas, 1936. *Bull. Br. Mus. Nat. Hist. (Zool.),* 58(1): 21-36.

GUZMÁN A.F. & POLACO O.J., 2002. - Hiperostosis en peces mexicanos. *Archaeofauna*, 11: 45-62.

HEWITT R.A., 1983. - Teleost hyperostoses; a case of Miocene problematica from Tunisia. *Tertiary Res.*, 5: 63-70.

JOHNSON C.R., 1973. - Hyperostosis in fishes of the genus *Platycephalus* (Platycephalidae). *Jpn. J. Ichthyol.,* 20: 178.

KORSCHELT E., 1940. - Über Besonderheit im Aufbau des Knochenfischskelets. *Z. Wissens. Zool.,* 152: 507-546.

KÖSTLER M., 1882. - Die Knochenverdickungen am Skelett von Knochenfischen. *Z. Wissens. Zool.*, 37: 427-456.

LAROCHE J., PERON M. & LE GAL Y., 1982. - Étude de l'hyperostose vertébrale et crânienne chez deux téléostéens *Trachurus trachurus* et *Trachurus mediterraneus*, par la diffraction des rayons X et l'incorporation de 45 Ca. *C. R. Acad. Sci., Paris*, 294: 1045-1050.

LINDSEY C.C., 1978. - Form, function and locomotory habits in fish. *In*: Fish Physiology 7 (Hoar W.S. & Randall D.J., eds), pp. 1-101. New York: Academic Press.

MEUNIER F.J. & DESSE G., 1986. - Les hyperostoses chez les Téléostéens : description, histologie et problèmes étiologiques. *Ichthyophysiol. Acta*, 10: 130-141.

MEUNIER F.J. & DESSE J., 1994. - Histological structure of hyperostotic cranial remains of *Pomadasys hasta* (Osteichthyes, Perciformes, Haemulidae) from archeological sites of the Arabian Golf and the Indian Ocean. *In*: Fish exploitation in the past, Proc. 7th Meeting ICAZ Fish Remains Working Group (Van Neer W., ed.). *Ann. Mus. R. Afr. Cent., Sci. Zool.*, 274: 47-53.

MEUNIER F.J. & GAUDANT J., 1987. - Sur un cas de pachyostose chez un poisson du Miocène terminal du bassin méditerranéen, *Aphanius crassicaudus* (Agassiz), (Teleostei, Cyprinodontidae). *C. R. Acad. Sci., Paris*, 305: 925-928.

MEUNIER F.J. & RAMZU M., 2006. - La régionalisation morphofonctionnelle de l'axe vertébral chez les Téléostéens en relation avec le mode de nage. *C.R. Palevol.*, 5: 499-507.

MEUNIER F.J., BÉAREZ P. & FRANCILLON-VIEILLOT H., 1999. - Some morphological and histological aspects of hyperostosis in the Equatorian marine fish *Prionotus stephanophrys* (Teleostei, Triglidae). *In*: Proc. 5th Indo-Pacific. Fish Conf., Nouméa, 1997 (Séret B. & Sire J.Y., eds), pp. 125-133. Paris: SFI.

OLSEN S.J., 1969. - Hyperostosic fish bones from archaeological sites. *Archaeol. Soc. New Jersey Bull.*, 24: 17-20.

OLSEN S.J., 1971. - Swollen bones in the Atlantic cutlass fish *Trichiurus lepturus* Linnaeus. *Copeia*, 1: 174-175.

SCHLÜTER T. & KOHRING R., 2002. - Palaeopathological fish bones from phosphorites of the Lake Manyara area, Northern Tanzania. Fossil evidence of a physiological response to survival in an extreme biocenosis. *Environ. Geochem. Health*, 24: 131-140.

SCHLÜTER T., KOHRING R. & MEHL J., 1992. - Hyperostotic fish bones ("Tilly bones") from presumably Pliocene phosphorites of the Lake Manyara area, Northern Tanzania. *Paläont. Zeit.*, 66(1-2): 129-136.

SELVARAJ G.S.D., GOPAKUMAR K. & RAJAGOPALAN M., 1973. - On the occurrence of osteochondroma and osteoma in the marine catfish *Tachysurus jella* (Day). *J. Mar. Biol. Ass. India*, 15: 571-576.

SMITH-VANIZ W.F., KAUFMAN L.S. & GLOVACKI J., 1995. - Species-specific patterns of hyperostosis in marine teleost fishes. *Mar. Biol.*, 121: 573-580.

SMITH-VANIZ W.F. & CARPENTER K.E., 2007. - Review of the crevalle jacks, *Caranx hippos* complex (Teleostei: Carangidae), with a description of a new species from West Africa. *Fish. Bull.,* 105: 207-233.

STARKS E.C., 1911. - Osteology of certain scombroid fishes. *Stanford Univ. Publ., Univ. Ser.*, 5: 1-49.

TREWAVAS E., 1936. - Dr Karl Jordan's expedition to South-West Africa and Angola: the freshwater fishes. *Nov. Zool., Tring*, 40: 63-74.

TYLER J.C., PURDY R.W. & OLIVER K.H., 1992. - A new species of *Sphoeroides* pufferfish (Teleostei: Tetraodontidae) with extensive hyperostosis from the Pliocene of North Carolina. *Proc. Biol. Soc. Washington*, 105: 462-482.

WEBB P.W., 1978. - Hydrodynamique et énergétique de la propulsion des poissons. *Bull. Office Rech. Pêch. Can.*, 1-160.

WEILER W., 1973. - Durch Hyperostose verdickte Fischknochen aus dem oberen Sarmat von Nord-Carolina, USA. *Senckenbergiana Lethaea*, 53: 469-477.

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